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Final Performance Report

Introductory Remarks:

The project focused on the infrared (IR) sensory systems of so-called pyrophilous beetles

which show the behaviour to approach forest fires. For this reason, the beetles are equipped

with IR sensory organs. Compared with uncooled technical IR sensors, the insect IR receptors

have some major advantages: (i) there is no need for temperature constancy; (ii) the receptors

operate at high ambient temperatures; (iii) the receptors are rugged having a smart design, and

work under harsh environmental conditions. Additionally, the neuronal network which

processes the IR information in the central nervous system of the beetles, obviously can

extract the relevant signals from considerable noise.

The objective of the proposed research was to broaden our understanding of the biological

significance, special function, and performance of biological IR reception. This included the

search for hitherto unknown IR receptors in pyrophilous insects. The final aim of the research

was to further develop and improve a technical uncooled IR sensor and the appropriate signal

processing algorithms which are based on the principles and mechanisms of its biological

models which were improved by millions of years of evolution.

To achieve the objectives, morphological, behavioural, neurophysiological, and thermo-

physical investigations have been performed. Using the obtained results, the prototype of the

photomechanic IR detector had been improved by combining appropriate solid absorbers with

sensitive mechanosensors. Additionally, an approach was made to determine some important

parameters, which are used to specify technical IR sensors.

People involved in this research:

Dr. Helmut Schmitz: PI

Three graduate students finished their diploma theses under this grant.

I. The prothoracic infared organs of pyrophilous beetle *Acanthocnemus*nigricans (Acanthocnemidae)

During the term of the grant a hitherto unknown IR receptor was discovered in the Australian "little-ash" beetle *Acanthocnemus nigricans* (family Acanthocnemidae)

Acanthocnemus nigricans is a small dark beetle having a body length of only 3-6 mm. The species nigricans is the only recent species within the genus Acanthocnemus and is distributed all over Australia. In contrast to its inconspicuous appearance, A. nigricans shows a remarkable behaviour as beetles of both sexes are attracted by forest fires. The beetles invade a freshly burnt area immediately after the flames are extinguished and approach areas where glowing remnants of trees or hot ashes are still present. The reason for this so-called pyrophilous behaviour is hardly understood but it can be speculated that the described "hot spots" serve as meeting places for the sexes. Most probably, the females deposit their eggs into the ash or under the bark of burnt trees. Currently, the larval food is unknown. Because larvae were obviously exported out of Australia inside wood, it is very probable that the cambium layer of freshly burnt trees represents the primary source of food for the first instars.

Nothing was known about heat receptors in A. nigricans. However, a pair of unusual hypomeral structures in front of the fore coxae has been described (Lawrence and Britton 1994). Each structure consists of a tiny cuticular disc (diameter 100-150 μ m) which could serve as an absorber for electromagnetic radiation. We subjected these structures to in-depth morphological and physiological investigations with respect to a possible fire-relevant sensory function. By our morphological and ultrastructural investigations, we were able to describe a new type of insect sensillum which most probably is involved in IR reception.

Material and methods

Animals

Adult beetles were collected in 2002 and 2003 on freshly burnt areas in Western Australia. Animals were kept for several weeks in plastic boxes and fed with raisins, peanuts and walnuts; drinking water was given ad libidum.

Scanning electron microscopy

12 beetles were air-dried and glued on holders by Leit-Tabs (Plano, diameter 12 mm) with either the dorsal or the lateral side. Sensory discs from 7 beetles were isolated and cleaned by sonication in a mixture of chloroform / ethanol (2:1) for 2 min. Discs were air-dried again and mounted on holders in an upright position which allowed examination from all sides. Specimens were sputtered with gold and examined with a Cambridge Stereoscan 200 SEM.

Light and transmission electron microscopy

Sensory discs of 10 beetles were isolated and immediately immersed in iced glutaraldehyde fixative (3% glutaraldehyde in 0.05 mol 1^{-1} cacodylate buffer, pH 7.1; osmolarity 380-400 mosmol 1^{-1}) and fixed overnight. The discs were then washed in buffer, postfixed with 1.5% OsO₄ in the same buffer, dehydrated through an ascending ethanol series and embedded in Epon 812. Semithin and ultrathin sections were cut with a Reichert Ultracut Microtome using glass- or diamond knives. Semithin sections (0.5 μ m) were stained with a 0.05% toluidine-blue/borax solution and examined with a Leitz DM RBE light microscope. Digital images of the sections were taken with a Nikon Coolpix 5000. Ultrathin sections were stained with uranyl acetate and lead citrate and examined with a Zeiss EM 109 TEM.

3D-reconstruction of the sensory disc

To investigate the number and position of sensory cell somata inside the sensory disc, a series of 210 semithin cross-sections was cut through a sensory disc. The digital images of the sections were stored on a PC and the software Amira (Version 3.0, TGS Inc., San Diego, USA) was used for 3D reconstruction. Due to inferior quality, 35 out of the 210 images could not be used. Therefore, the distances between images were adjusted individually to compensate for the loss of those sections. The outer cell membranes of the somata could not be traced and identified reliably. Therefore, we used the nuclei and nucleoli of the sensory cells for soma identification. To guaranty automatic identification by the software, nuclei and nucleoli as well as the cuticle were coloured in each section using a digitizing tray.

Electrophysiology

Extracellular electrophysiological recordings were performed form prothoracic discs from 4 beetles by electrolytically sharpened tungsten electrodes which were gradually driven into the cuticle of the disc by a micromanipulator. To minimize damage of the disc by the electrode,

penetration of the cuticle was stopped as soon as neuronal activity of the spontaneously active units was encountered. Signals were amplified 1000 x and displayed on an oscilloscope. In order to mimic the natural stimulus (i. e. a forest fire), we stimulated the IR organ with a small thermal emitter which was mounted 40 mm away from the beetle and could be heated to 400 ° C. The beetle was glued with its ventral side up onto a plate and a shutter between the hot emitter and the beetle allowed defined exposure to the diffuse thermal radiation. The twodimensional surface of the emitter, turned towards the beetle, was 0.7 x 2.5 cm. In a series of experiments we irradiated the prothorax with the sensory disc for 1 sec. To estimate the corresponding increase in cuticular temperature, we used a tiny thermocouple (Type K: Chromega/Alomega, diameter of the bead 33 µm). Because it was technically impossible to mount the bead under the outer cuticle of the intact sensory disc, we glued it with a minimal amount of Syndeticon to the inner surface of a piece of abdominal cuticle of an air-dried beetle. As the abdominal cuticle (about 15 µm) is twice as thick as cuticle from the outer side of the sensory disc (7 - 8 µm), temperature values might be slightly underestimated. The wires of the thermocouple were connected to an electronic thermometer (HH 202, Newport Omega, accuracy + 0.2° C) and the cuticle was exposed to the thermal emitter from a distance of 40 mm. Mean temperature increase of the cuticle was 4.7° C + 0.7° C (n = 8 exposures).

Results

The prothoracic IR organs

One pair of IR organs is located on the prothorax in both sexes. The two organs are situated directly anterior to the coxae of the prothoracic legs (Fig. 1). The most striking component of an IR organ is a more or less round cuticular disc which is somewhat sunken into the surface of the prothorax. At its posterior edge, the disc is held by a stalk which originates at the dorso-anterior border of the coxal cavity. Below the disc, a hemispherical air-filled cavity is situated. Because the opening of the cavity is somewhat larger than the diameter of the disc, exchange of air between the cavity and the outside is possible. The disc, which has been found to be innervated by sensory cell somata (Schmitz et al., 2002) represents the actual IR receptor, whereas the cavity can be regarded as an auxiliary structure.

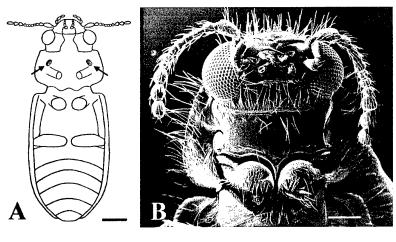


Fig. 1

Outer morphology of the sensory disc

A sensory disc has a diameter between 110 and 185 μm . The size roughly correlates with the size of the beetle. In some beetles, the outer surface appears slightly curved inward whereas the surface of the underside always is bulged out convexly (Figs. 2B-D). The stalk shows an oval cross section with an inner diameter of about 30 μm . We found no indication that the stalk has any flexible properties.

Numerous small sensilla can be found on the outer surface of the disc (Fig. 2B). However, the sensilla are not evenly distributed. Most sensilla concentrate within an anterior semicircular area on the upper surface. Some sensilla (about 13 %, N=9 discs) were even found on the anterior edge of the disc (Figs. 2C). We never found a sensillum on the underside. Most probably, all sensilla belong to the same type and can be identified by their cuticular apparatus which consists of a small cuticular peg surrounded by a socket. At its base, the peg has a diameter of about 2 μ m and a total length of about 3 – 5 μ m.

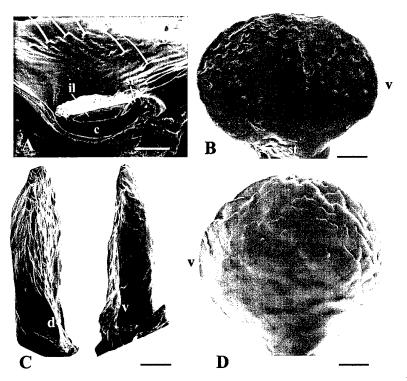


Fig. 2

Morphology and ultrastructure of the sensilla

Series of cross and longitudinal sections through the sensilla revealed, that the small cuticular peg consists of massive cuticle. Neither pores nor a lumen inside the peg was found. From below, the peg is innervated by a single ciliary receptor cell (see reconstruction of a sensillum in Fig. 3). The dendritic outer segment (DOS) is cylindrically and unbranched. The DOS has a diameter of less than 0.5 µm and contains only sparse neurotubuli. As a specific feature, the entire DOS in ensheathed by an electron dense material which most probably is the hypertrophied dendritic sheath. The outermost tip of the DOS terminates at the base of the peg and is connected to its cuticle by the presumed dendritic sheath which – at least in some sections - seems to insert into the basal part of the peg. No tubular body was found. A ciliary constriction subdivides the dendritic outer (DOS) and the dendritic inner segment (DIS). However, because the DOS shows already a small diameter, there is no decrease in diameter from the basal part of the DOS towards the dendritic constriction. Two basal bodies were found just below the constriction. The basal bodies were interconnected by root filaments which do not extend much further into the proximal region of the DIS. Below the ciliary constriction the DIS strongly broadens. As a predominant feature, many deep invaginations of the cell membrane into the lumen of the cell were observed. Thin, leaflike

processes of glial cells are squeezed between the membranes and a large number of mitochondria were always found inside the DIS.

The soma region could be easily identified by a large nucleus but the DIS and the soma are not clearly distinguishable as they show the same structural features (i.e. thin but deep invaginations of glial cells into the cell lumen and lots of mitochondria). We found 2 - 3 enveloping cells (most probably representing the thecogen, trichogen and tormogen cell) which mainly enwrap the dendrite and the distal region of the soma cell. Consequently, most of the cell soma is enveloped by a thin glial layer. In general, 2 - 3 nuclei of enveloping cells were found in the region of the ciliary constriction. Due to the extreme entanglement of cell material inside the disc, an unequivocal identification of single enveloping cells could no be made. Based on complete series of ultrathin sections through a total of 5 sensilla, a graphical reconstruction of a single sensillum was made (Fig. 3).

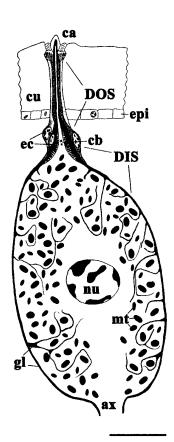
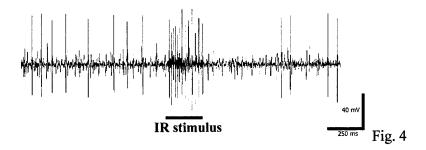


Fig. 3

First electrophysiological recordings from the multipolar neurones inside the disc

The recordings from the sensory disc (N = 4 beetles) showed that the multipolar neurons had ongoing activity at room temperature. The frequency of spontaneous activity of single units was between 5 and 10 Hz and was unaffected by sound (voice or hand clapping), moderate air movements or gentle touch of the surrounding cuticle by a bristle. In contrast, exposition to the IR radiation from the thermal emitter increased firing frequency in a phasic-tonic way (Fig. 4). We also stimulated the receptor with warm air and visible light from a red-light helium-neon laser, which was used in former studies to stimulate the IR organs of pit vipers. Independently of how the temperature was increased, an increased spike frequency resulted. In general, a higher steady-state temperature was coded by a higher discharge frequency of the units. Cessation of the stimulus inhibited the generation of action potentials.



SUMMARY: *A. nigricans* has one pair of unique prothoracic sensory organs which most probably serve as infrared receptors. Each organ consists of a cuticular disc which is fixed over an air-filled cavity. On the outer surface of the disc, about 90 tiny cuticular sensilla are situated. The poreless outer peg of a sensillum is 3 – 5 μm long and is surrounded by a cuticular wall. One ciliary sensory cell innervates the peg, the dendrite of which is divided into an outer and an inner dendritic segment. A tubular body could not be found in the outermost dendritic tip. As a special feature, the outer dendritic segment is enveloped by an electron-dense mantle, which most probably represents the hypertrophied dendritic sheath. The inner dendritic segment and the soma are fused indistinguishably forming a common cellular space. Thin, leaflike extensions of glial cells deeply extend into that enlarged lumen which also contains large numbers of mitochondria. The sensilla of the sensory disc of *A. nigricans* obviously represent a new type of insect sensillum of hitherto unknown function. First electrophysiological investigations indicate that they may function as warm receptors.

Publications:

H. Schmitz, A. Schmitz, S. Trenner, H. Bleckmann (2002) A new type of insect infrared organ of low thermal mass. *Naturwissenschaften* **89**: 226-229

E. Kreiss, A. Schmitz and H. Schmitz: Morphology of the specialized sensilla in the prothoracic sensory organ of *Acanthocnemus nigricans* (Coleoptera, Acanthocnemidae) *Arthropod Structure and Development* [submitted for publ.to *Arthropod Structure and Development*]

Student thesis: Diploma thesis of graduate student Eva Kreiss (finished in August 2003) [Title: Funktionsmorphologische Charakterisierung der spezialisierten Sinneszellen des prothorakalen Infrarotorgans von *Acanthocenus nigricans* (Coleoptera, Acanthocenidae; Diplomarbeit, 2003, Institut für Zoologie, Universität Bonn]

II. Physiology and evolution of the infrared receptors of pyrophilous beetles of the genus *Merimna*

A thermosensitive multipolar neuron innervates each of the four abdominal IR receptors of the Australian buprestid beetle *Merimna atrata*. Electrophysiological recordings showed that the neuron is active within a broad range of body temperatures (tested between 10° C and 40° C). We heated the receptors with a red diode laser ($\lambda = 0.66 \, \mu m$) at intensities ranging from 5.3 mW/cm² up to 1.3 W/cm². In general, warming caused an increase of receptor activity. Peak discharge frequencies were reached 100 to 300 ms after onset of irradiation. After peak frequencies were reached, distinct adaptation took place within seconds (Fig. 5). A linear increase in irradiation intensity caused an exponential increase in peak frequencies. Lowest threshold was found to be at $40 \, \text{mW/cm}^2$ where latencies were $47 \, \text{ms}$. At the highest intensity tested (1.3 W/cm²), peak frequencies increased up to about 300 Hz and latencies decreased to 24 ms.

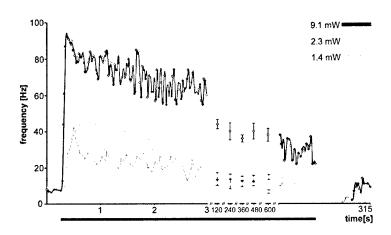


Fig. 5

Considering the pyrophilous behaviour of *Merimna* and the morphological data from our previous studies, our results strongly support the hypothesis that the abdominal receptors are infrared receptors. We also recorded the responses of the photomechanic infrared sensilla of *Melanophila acuminata* under the same experimental conditions. These results show that the photomechanic sensillum of *Melanophila* has a higher sensitivity, and that the latencies are considerably shorter (Fig. 6).

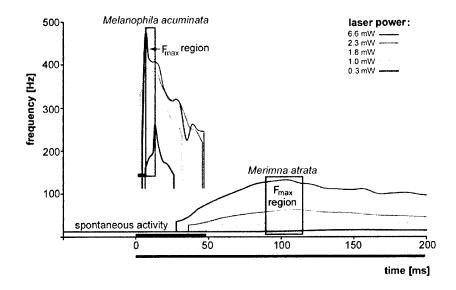


Fig. 6

The smallest increase in temperature which can be resolved by the multipolar sensory cell in the *Merimna* IR receptor is 0.08 ° C. This is the increase in temperature which can be evoked by irradiating the receptor for 200 ms with 0.6 mW (= 40 mW/cm²). On the other hand, the receptor tolerates very high intensities. Our 20 mW Laser was not strong enough to drive the

receptor into saturation, which probably is reached at a frequency of about 500 Hz (calculation based on a duration of 1 ms each of the action potential and the refractory period). Based on temperature measurements at the cuticle of the IR receptor we concluded that a frequency of 500 Hz is reached at an intensity of 2 W/cm². In this case, the dynamic range of the *Merimna* receptor would be about 34 dB.

In *Melanophila* we determined a threshold sensitivity of 5.3 mW/cm² which corresponds well to previously published data (cf. Schmitz and Bleckmann 1998). Behavioural experiments have revealed that *Melanophila acuminata* can perceive even weak IR radiation at an intensity of about 100 µW/cm² (Evans 1966). Thus *Melanophila* beetles may use their IR receptors for the detection of forest fires from greater distances. The lower sensitivity of the *Merimna* receptor indicates that *Merimna* does not use its presumed IR receptors for the detection of remote forest fires but rather to prevent the beetle from landing on a hot surface.

Most individuals of the Australian "fire-beetle" *Merimna atrata* have two pairs of IR receptors which are located ventrolaterally on the second and third abdominal sternite. An IR receptor consists of a specialized IR absorbing area which is innervated by a neural complex. This complex contains one thermoreceptive multipolar neuron with a unique terminal dendritic mass (TDM) and two scolopidia and was termed "sensory complex". However, also individuals with one pair of IR receptors on the second sternite and beetles with three pairs on the second, third, and fourth sternites were found. Additionally, beetles having one or two pairs of IR receptors may have preliminary stages of IR receptors on the third and fourth sternite, respectively. We found two kinds of preliminary stages, both of which are characterized by a much less pronounced absorbing area (Fig. 7). In all five abdominal sternites segmental nerves are attached to the cuticle with a neural complex. Investigation of complexes of non-IR sternites suggest that the sensory cells inside the sensory complex of an IR receptor have developed from common internal stretch receptors. From our results it can be hypothesized that the IR sensory system in *Merimna atrata* has not yet reached a stage which can be regarded as evolutionary stable.

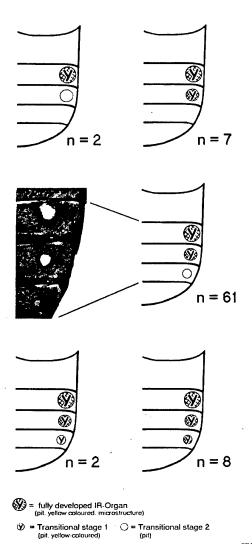


Fig. 7: 80 beetles investigated

Publications:

H. Schmitz and S. Trenner (2003) Electrophysiological characterization of the multipolar thermoreceptors in the "fire-beetle" *Merimna atrata* and comparison with the infrared sensilla of *Melanophila acuminata* (both Coleoptera, Buprestidae). *J. Comp. Physiol.* A, **189**: 715 - 722

T. Mainz, A. Schmitz and H. Schmitz (2004) Variation in number and differentiation of the abdominal infrared receptors in the Australian "fire-beetle" *Merimna atrata* (Coleoptera, Buprestidae). *Arthropod Structure and Development* [in press]

Student thesis: Diploma thesis of graduate student Tobias Mainz (finished December 2002)

[Title: Morphologische und physiologische Untersuchungen zur variablen Ausprägung der abdominalen Infrarotrezeptoren des australischen "Feuerkäfers" *Merimna atrata* (Coleoptera, Buprestidae), Diplomarbeit, 2002, Institut für Zoologie, Universität Bonn]

III. Behaviour of pyrophilous Australian beetles at wildfires

In Australia, organisms are exposed to fires since millions of years. This long-lasting evolutionary pressure has caused many endemic plants to evolve special morphological and physiological adaptations to cope with fires. Well known examples are several species of the Banksia trees and of the balga grasstrees.

Much less is known that also some insects have adapted to frequent fires and therefore can be found more frequently on burnt than on unburnt land: those insects are called pyrophilous. Some of those insects are already attracted by open flames, by hot ashes or by smoke. One reason for this unusual behaviour is that insects or their offspring highly depend on food resources which are made available by the fire. Such food can be the wood of the freshly burnt trees or special ascomycete fungi which start to grow on the freshly burnt soil or wood immediately after the flames have subsided. When removing the black charcoaled bark of a burnt tree, it is astonishing to see that the wood itself is intact. However, the water content is considerably reduced. As insects are able to gain water by metabolic processes, a variety of wood boring insect larvae are known that can develop in dry wood. Therefore, the burnt wood is a valuable food source for some specialized insect species.

Each February in 2002 to 2004 we had the chance to investigate the behaviour of two species of pyrophilous "fire-beetles" on freshly burnt areas in Western Australia around Perth. During our stay we gained new insight into the behaviour and into the sensory physiology of these highly specialized insects.

The big Australian "fire-beetle" Merimna atrata

When a large bushfire is raging, *Merimna atrata* approaches the fire in sometimes unbelivable masses. The reason for the unusual behaviour is known: the whole reproduction cycle of *Merimna* is totally dependent on bushfires. First, the fire serves as a meeting place for males

and females. Secondly, the wood-boring larvae can only develop in the wood of freshly burnt Eucalyptus trees. When a bushfire takes place, the behaviour of the large beetles can easily be observed: the beetles invade the steaming burnt area as soon as the flames of the running fire have gone over the vegetation. Most beetles can be found sitting or running over the charred bark of the burnt trees. Now it becomes obvious why *Merimna* is coloured black: it is perfectly adapted to the predominant surface colour of its special habitat. Males look for females, and copulations can be frequently observed. Finally, females deposit their eggs under the bark of the burnt trees. We also have observed that beetles search for food and inspect crevices in the bark or in the burnt soil in order to find something to eat. Sources of food can be other scorched insects or even dead small vertebrate animals but also edible plant material like fruits and seeds which were not burnt to ashes.

A freshly burnt area bears many risks, not only for a beetle. There are a lot of "hot spots" where high temperatures can be encountered. Often it cannot be decided visually if the surface of a tree or of the ground has a dangerous high temperature or not. But *Merimna atrata* safely evades to land on such a hot spot: we never found a beetle injured or killed by hot surfaces. This obviously is the reason why *Merimna* has evolved IR receptors.

The small Australian "little-ash beetle" Acanthocnemus nigricans

When inspecting a freshly burnt area some hours or even a few days after the fire, we concentrated on localities where hot ashes or glowing remnants of trees could be encountered. Near those "hot spots" we took a closer look at the ground or on the black bark of trees. And indeed, not only many *Merimna atrata* could be observed but also a much smaller, rather inconspicuous beetle of only 3 to 5 mm in length: *Acanthocnemus nigricans*. In contrast to *Merimna atrata*, *Acanthocnemus* shows a very cryptic behaviour: this beetle quickly runs over the burnt ground or the bark of trees for a short time and then seeks shelter in little crevices for many minutes. We speculate that this behaviour has evolved because *Acanthocnemus* is a potential prey of *Merimna*. The reason for the presence of *Acanthocnemus* on a freshly burnt area is nearly unknown. In the meantime, we have a lot of evidence that the fire also attracts males and females and that the area around hot spots serves as a meeting place for the sexes. We also have observed few copulations. On the other hand no information is available about the food resources of the beetles and their larvae. It can be speculated that the larvae also feed on freshly burnt wood or even that they depend on special ascomycete fungi which start to grow pretty soon on burnt soil or wood.

Concluding remarks

It is always impressive to observe how perfectly the two species of Australian "fire-beetles" are adapted to their hot and steamy environment. We never observed that a beetle became a victim of the heat. Despite we begin to understand some basic features of the sensory physiology of the pyrophilous beetles, a large number of problems still remains. At this point the two most interesting questions should be raised: (i) Why are the IR receptors of the beetles so different? (ii) Which other senses like vision or olfaction are involved in the detection of fires and in the recognition of hot spots on a burnt area? We hope to be able to give some answers in the near future.

Publication:

H. Schmitz and A. Schmitz (2002) Australian fire-beetles. LANDSCOPE 18(1): 36-41

IV. Building of a technical photomechanic IR detector

In contrast to the bolometer principle that is widely used in technical applications, the photomechanical principle employed by *Melanophila* beetles was unknown to engineers. In a photomechanical IR detector, a solid IR absorber is directly connected to a sensitive mechanosensor. It is important that the absorber molecules show strong stretch resonances in the IR wavelength range intended to be detected. This design automatically provides a high spectral sensitivity. Comprehensive information about IR absorption of materials can be accessed in the vast literature dealing with IR spectroscopy.

To demonstrate that an IR sensors based on a photomechanic principle can easily be built we fabricated and improved a sensor prototype (Fig. 8). This prototype, whose material value is less than about 3 Dollars, already detects IR radiation that has an intensity of less than 50 μ W/cm². First calculations have yielded a preliminary value for the standardized detectivity (D*, the most important parameter used to specify IR sensors) of 6 x 10⁶ cm Hz $^{1/2}$ W $^{-1}$ (Fig. 9). This value is about two to three orders of magnitude below the D* values of currently available uncooled technical microbolometers. However, it should be mentioned that our prototype is far from being optimized. Miniaturization of single sensory elements will reduce their thermal mass and thus will increase their sensitivity. Miniaturization in addition will allow the construction of multisensor arrays, a prerequisite for thermal imaging. Because the absorber material can be chosen according to the IR

wave lengths of interest, photomechanic IR sensors can be used in all ranges of applications where current IR sensors are utilized, e.g. for the detection of fires or hot surfaces as well as for the detection of animate and inanimate objects whose temperature differs from ambient and background temperature. Because photomechanic IR sensors are cost effective and robust, they may have a promising chance on the market.

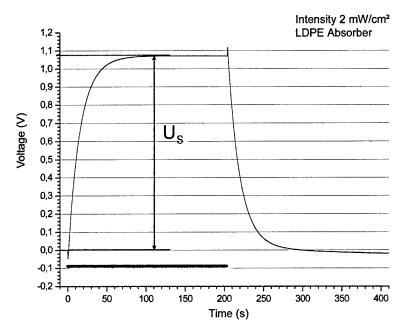


Fig. 8: Sensor signal

Parameters:

 $R = \frac{U_{S}}{E_{\text{eff}} \cdot A}$

Noise Equivalent $NEP = \frac{E_{\text{eff}} \cdot A \cdot U_{N}}{U_{S}}$ Power

Detectivity $D = \frac{1}{1000}$

Normalized $D^{\star} = \frac{\sqrt{\Delta f} \cdot \sqrt{A_{Absorber}}}{NEP}$

	Absorber		
	Teflon	LDPE	
A _{Absorber} (cm ²)	0,64	0,64	
E _{eff} (W/cm²)	0,0100	0,0100	
∆f (Hz)	1000	1000	
U _s (V)	0,53	1,072	
U _N (V)	6,14E-04	6,95E-04	
τ (s)	25,4	16,5	
R (V/W)	83,71	169,31	
NEP (W)	7,33E-06	4,10E-06	
D (W ⁻¹)	1,36E+05	2,44E+05	
D* (Hz ^{1/2} cm W ⁻¹)	3,44E+06	6,15E+06	

Fig. 9

Publications:

H. Bleckmann, H. Schmitz and G. von der Emde: Nature as a model for the building of artificial sensors. *J. Comp. Physiol.* A [in press]

Student thesis: Diploma thesis of graduate student Martin Mueller (finished September 2003) [Title: Thermophysikalische Untersuchungen an biologischen und technischen Infrarotdetektoren und Optimierung eines photomechanischen Infrarotsensors. Diplomarbeit, 2003, Naturwissenschaftlich-Technische Fakultät III, Universität des Saarlandes, Saarbrücken]